THE REPRODUCTIVE FUNCTIONS OF THE ARMY-ANT QUEEN AS PACE-MAKERS OF THE GROUP BEHAVIOR PATTERN

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Although they are among the commonest ants encountered in the tropical forests of the Old and New Worlds, the dorylines have long remained among the least known. In Africa and Asia the "driver ants" and in tropical America the "legionary" or "army" ants of this subfamily present many intriguing problems, especially in the predatory raids and nomadic life of their colonies and the biological status of their huge wingless fertile females, the dichthadiigynes. These last individuals are not very well known to science, since up to a relatively short time ago virtually no precise information was available concerning their relations to the colony. Actually we find, beyond propagative functions which differ rather strikingly in some respects from those of fertile females in other insects, the properties of the doryline queen make her a factor of critical importance in the general process of colony behavior.

This paper is directed toward accounting for the essential ontogenetic basis of the behavior pattern characteristic in the subgenus *Eciton s. str.*, an American branch of the subfamily Dorylinæ. Our study specifically concerns these terrestrial army ants, especially the type species of the subgenus, *E. hamatum.* The results may prove eventually to have relevance among the dorylines far beyond the conditions of the species on which this report is based.[2]

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The chief characteristics of the behavior pattern of *E. hamatum* involve the formation of bivouacs, raiding, and bivouac-change movements which in series may be termed migrations. In this species the temporary nest or bivouac of a given colony is a more or less cylindrical mass formed by the clustered bodies of ants alone, without foreign materials, usually depending from a log or vines, or hanging against a tree. From his studies in the rainy season the writer (1933; 1938) has described two distinctive conditions through which colonies of *E. hamatum* pass successively in alternation at such times: the *nomadic* and the *statary* activity phases. Roughly, each phase lasts close to 20 days before it is succeeded by the other. The principal characteristics of the nomadic phase are 1) highly developed daily raids and 2) a regular change of the bivouac site at the termination of each day. In rather sharp contrast, the statary phase is marked by 1) less developed raids and 2) occupancy of the same bivouac site throughout the interval. In addition there are other features which characterize each of these behavior phases. These are essentially intrinsic to the colony, yet as we shall find they are intimately involved in the entire system of events in Eciton behavior.

Our essential hypothesis is that a close relationship exists between behavior outside the bivouac (*i.e.*, raiding and bivouac-change processes) and conditions within the bivouac, and that this pattern of events basically depends upon the functions of the reproductive agent of the colony. Accordingly in this paper attention focusses upon the rôle of the mother queen, whose properties apparently are of key importance in the entire mechanism of the Eciton behavior pattern.

Material for this study was gathered and most of the field observations were carried out on Barro Colorado Island in the Panama Canal Zone, in the rainy season months of 1936 and 1938 (May to September). In that locality the rainy period usually begins in April and ends in early December. Investigations of the Eciton problem have yet to be conducted in the dry season. This limitation is important, since it is very probable that rainy-season conditions are optimal for the appearance of relationships such as we shall describe. In an indirect manner the results of this study suggest that with extreme changes in prevalent atmos-

pheric conditions important variations may occur in the described behavior pattern. In view of this, it is a fact of some importance that our evidence was gathered in a portion of the Caribbean lower rain-forest zone in which the rainy and dry seasons are differentiated rather sharply from year to year. What differences will be found under more variable meteorological conditions represent an interesting problem.

PROPERTIES OF THE ECITON QUEEN

From the time André (1885) captured the first dichthadiigyne from the subterranean bivouac of an *E.* (*Labidus*) *coecum* colony the list of captures has grown very slowly, and although fertile females are at present known from nearly 25 of the more than 100 recorded species of *Eciton* and all of the eight recorded species of *Eciton s. str.* (Bruch, 1934), they are still among the most highly prized collector's items. In view of the great difficulty of capturing them, it is scarcely surprising that these rare insects have been almost invariably clapped into alcohol when taken, under the influence of what Creighton has appropriately termed "collector's itch." This practice of course has not precluded the accumulation of much valuable information concerning the external morphology and the taxonomic affinities of the specimens; yet it has unfortunately kept in the remote background several important questions which can find their answers only in study of the living queen.

Thus it is unfortunate that from the records of more than a score of collections very little can be learned about the behavior and biological properties of the living individual. With the exception of general observations carried out by Wheeler (1900) with captive colonies of *E. schmitti* in Texas, no special investigations have been attempted. The present study stems from a general investigation of army-ant behavior which has revealed the probability that the dichthadiigyne plays a crucial though indirect rôle in the phenomena of Eciton behavior (Schneirla, 1934; 1938).

Eciton queens may be found in either of two very different conditions, the "normal" or contracted condition and the physogastric or egg-producing condition (see Fig. 1). For the present study, the dichthadiigyne material comprised 13 queens of *E.*

hamatum and one of *E. burchelli* in the contracted condition, and one queen of *E. hamatum* in the physogastric condition.   In each case, field notes on the colony from which a given queen was taken covered the general situation of the colony and its behavior (especially its raids and bivouac-change movements) over a period of days, the status of the brood or broods and the condition of the queen at the time of capture.   Each queen was kept alive in the laboratory as long as possible after capture, for observation and test both alone and in relation to the workers of her colony.

There is a notable disparity in our material as to condition of the queen when captured.   Why so many of the cases were in the contracted condition and only one case physogastric when taken will become clear as the general circumstances of Eciton life are disclosed.[3]   For a number of reasons, physogastric army-ant queens are exceedingly difficult to capture.   There is only one other case on record in which such an individual was observed during her short span of life in captivity, that of a physogastric queen of *E. (Labidus) coecum* taken by Weber (1941) in Trinidad.   Fortunately we are not forced to depend upon direct evidence concerning the queen at all stages, since an abundance of other evidence coordinates nicely with results derived from work on the queen herself.[4]

A descriptive contrast of queens and workers.—The Eciton queen (Fig. 1) stands out as strikingly unique among fertile insect individuals and as a highly distinctive member of her colony. We may use the queen of *E. hamatum* as example.[5]   Unlike the queens of virtually all other ants, she is wingless *throughout life.* In color she is almost uniformly ferrugineous mahogany, darker than the yellowish brown which characterizes the workers, and lacks the cephalic paleness of major workers.   She differs strik-

[3] It is a striking fact that among 16 captured queens representing ten *Eciton s. str.* species and sub-species, reported by various authors prior to 1942 (see *e.g.,* Wheeler, 1921; Bruch, 1934), *all* were in the contracted condition.

[4] In the present paper the supporting evidence is reported rather concisely. Further details and additional evidence will be incorporated in a monograph on this subject, now in preparation with the collaboration of Dr. Harold R. Hagan of the Department of Biology, City College of New York.

[5] The reader is referred to Wheeler's systematic descriptions of the first queens of *E. hamatum* (1925) and *E. burchelli* (1921) to be discovered.

ingly from the workers in gross size and in anatomical detail. The greater bulk of the queen is suggested by the fact that her over-all length (contracted) is close to 17.1 mm. (Av. 6 specimens), whereas the range of body length in the workers is 2.5 mm. (minor) to 9.5 mm. (major). The polymorphic worker types resemble the queen only very broadly, for example both queen and workers possess well-developed and dentate tarsal claws, near the inferior occipital corners of the queen's head there are small obtuse projections homologous to the acute spines of the worker major, and the queen possesses strikingly prominent pairs of epinotal and petiolar horns contrasting with two simple aligned nodes in the worker. Among many impressive morphological differences are the large lateral pseudo-ocelli (Werringloer, 1932) of the queen and the relatively tiny ones of workers, the great bulk of the queen's thorax and her well-developed legs as contrasted with corresponding slenderness in the worker's structures, and in particular the great size of the queen's abdomen contrasted with the much smaller gaster of the worker. Associated with an enormous expansion of reproductive functions in the queen and the probable absence of such functions in the worker, the hamatum queen's gaster even when contracted measures near 9.1 mm. in length and 5.5 mm. in its greatest width, whereas the gaster of the largest major worker measures only 2.6 mm. in length and 1.8 mm. in width. The queen's gaster terminates distinctively in a large triangular shelf, the hypogynium. Another striking characteristic of the queen is the marked development of her external respiratory orifices or stigmata, suggesting a high stage of development in the respiratory system generally.

This general morphological comparison may suffice to illustrate the extent to which the Eciton queen diverges from the workers, paralleling a functional specialization which correspondingly differs markedly from that of the workers. The nature and extent of the dichthadiigyne's specialization becomes clear when we consider some typical characteristics of her behavior and her place in the life economy of the colony.

Behavior and functional properties of the "normal" or contracted queen.—In *E. hamatum* and probably in *Eciton s. str.* generally the reproductive capacity of any given colony is cen-

tered in a single individual, a fecund dichthadiigyne. A selective mechanism of some kind evidently is involved which excludes additional queens, possibly at a time shortly before or after young queens are fertilized. Circumstances indicate that this one fecund individual must pass around nine-tenths of her days in the rainy season in the resting or contracted condition, which as a consequence may be termed her "normal" state. Ordinarily she
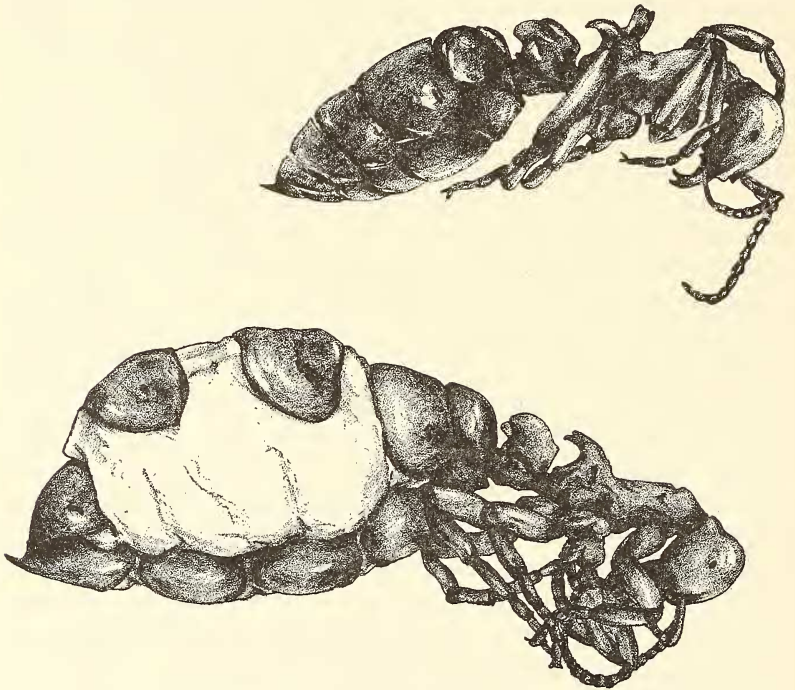

FIG. 1. Queens of *E. hamatum* in the contracted (upper) and the physogastric or gravid condition. (*Cf*. Fig. 2 and Table I.) Total length of the contracted queen, 17 mm. (Drawing by Miss Janet Roembild, from photographs by Dr. Virgil Argo, Dept. of Biology, City College of New York.)

does not leave the confines of the bivouac, except when she is drawn into a bivouac-change movement, an event that scarcely ever engages her before nightfall.

Circumstances indicate that the sequestration of the queen may be due largely to the effect which light exerts upon her. In laboratory tests she reacts specifically to directionalized bright light

by turning away from the source and moving energetically about until in darkness. Whenever she chances into the light, facing toward the source, the queen volte faces abruptly and runs off. (Among numerous observations, this test was repeated in one instance 12 times in 30 minutes with the same queen,—always with the described result.) When illumination is not intense the response is more variable, yet even then as a rule the queen settles down only when in a fairly dark part of the nest.

In contrast to the queen, the workers seem virtually incapable of specific orienting responses to light. They are aroused to activity by light after a period of darkness; thus colonies are regularly stimulated to begin their daily raiding after dawn (Schneirla, 1938; 1940). This however is a mere photokinetic effect (*i.e.*, a generalized excitation by light), and they appear incapable of orienting to directionalized illumination except in a very crude fashion as an outcome of restless movements over a considerable time. That the basis of this outstanding difference between queen and workers rests in different optoneural equipment is suggested by the fact that in *E. hamatum* the gross size of the queen's lateral pseudo-ocellus is more than twice that of the major worker's. We should expect to find correspondingly accentuated differences in the internal structure of the visual receptor, and in related mechanisms, underlying the queen's pronounced normal reactivity to light.[6]

This recalls the fact that the fertilized queens of ants in general are repelled by light. Whether the Eciton queen, like any others, is positive to light prior to fertilization cannot be said at present; however, the sharpness of the functional queen's avoidance response is clear. The basis of a highly adaptive circumstance is thereby provided—that the queen is cloistered in a well-protected situation except when the colony shifts its home site. The prevalence of this condition is attested by the fact that Eciton queens are never seen at other times, as during raids—its effectiveness is emphasized by the difficulties one experiences in capturing these queens.

[6] Although no queen material was available for Werringloer's (1932) valuable histological study of Eciton visual mechanisms, species differences were found in optic histology which appear to parallel typical behavior differences.

That the queen keeps to the bivouac in the daytime, during raids, is not attributable to any inability to follow the colony's trails. In the laboratory, captive hamatum queens may run for hours at a time in a column following a circular path established by workers or, when one is set down near a vacated trail of her own colony in the forest, she follows the route successfully once she hits upon it. Evidently it is her ''photophobic'' proclivities that mainly account for the queen's sequestration in the bivouac.

Although for a long time the idea has held sway that the army-ant queen is moved passively about by the workers when the colony shifts its site, in *Eciton s. str.* the facts are contrary to this sup-position. In laboratory nests the queen readily makes her way about despite the usual added burden of several workers hitch-hik-ing and dragging from her legs or gaster. The physical char-acteristics of her well-developed legs give every indication of great strength, as does her robust frame in general—an impression borne out fully by her behavior. The test comes during the long bivouac-change march in the wild when the queen must make her way over a route generally much longer than 100 meters, passing along a narrow and tortuous trail full of hazards such as vine bridges and sharp turns although she is swarmed under at nearly every step by a frenzied crowd of workers.

On a number of occasions the hamatum queen's participation in the colony movement has been observed, always at night except in two instances when colonies were greatly oversize and the move-ments unduly extended. The bivouac-change usually gets under way before dusk and is completed during the night, with the queen coming along during the latter part and frequently near the very end of the trek. The explanation seems to be that she is normally stationed in the innermost recesses of the cluster, cen-tered in the brood with a mass of workers minor around her, in a section of the bivouac which is likely to be almost the last to be drawn into the evacuation.

Just before the queen appears from the bivouac there is a very noticeable increase in excitement among the workers on the trail, agitated variable movement becomes common instead of the monotonous plodding seen previously, and the column begins to widen perceptibly from the 2–3 cm. which is characteristic. As

the column becomes more crowded it broadens to as much as 15 cm. within a few minutes, then the queen appears in the thickest part.   As the queen moves along she is not only surrounded by jostling workers of all sizes, but much of the time is literally covered with them, has them underfoot and hanging to her.   The workers hamper her movements particularly when she slows in mounting steep grades or in rounding sharp corners; at such times they may crowd around so that she is actually stopped for a time. The remarkable fact is that amid this great excitement and arduous labor the queen is able to follow the trail in its devious windings and through its difficult sections.[7]   Tests show that this ability depends upon a response to Eciton chemical.   For example, if the queen is taken up and returned to the route when there are no workers upon it, she follows it readily.   There can be little doubt about the fact that the queens of *Eciton s. str.* participate quite actively in the bivouac-change movements of their colonies and get to the new site under their own power.

The adaptive significance of the workers' behavior toward the queen during the lengthy migratory trek deserves mention.   Since at all times a high pitch of excitement is maintained in the queen's section of the march, any intrusion is immediately responded to by large numbers of frenzied workers so aroused that they bite and sting with very little provocation.   In the darkness of night, the feverish activity that prevails in the few meters of column near the queen contrasts strongly with the lethargic monotonous lock-step movement that prevails throughout the other sections of the movement.   Only in the entourage of the queen are the workers aroused to a degree of excitement and responsiveness that resembles their daytime activity in raiding.   The outcome is that the colony's reproductive specialist is well protected at the time when exposure is great.

The strength and vitality of the queen are shown impressively when the colony is etherized for capture.   Because of the agility and speed with which she is capable of moving when disturbed, the queen generally is able to make her escape from the bivouac while the principal mass of workers succumbs to the anaesthetic.

[7] Reichensperger (1934) observed similar occurrences in a bivouac-change movement of an *E. lucanoides* colony in Costa Rica from which he captured the queen.

Thus she is frequently discovered under a leaf or piece of bark near the outer edge of the sheet used to imprison the bivouac, still somewhat active although workers in numbers lie prone around her, and if the way is not blocked she may make good her escape along a raiding trail.

Wheeler (1921) has remarked upon the possibility that an extensive development in the respiratory system of the Eciton queen is an important adaptation to a sequestered bivouac life.   The pronounced development of this system in general is indicated by the prominence of the spiracles, the external openings of the breathing tubes.   With a highly efficient mechanism for gaseous exchange, it is possible for the queen, despite her huge bulk and relatively great oxygen needs, to remain for long times within the close air of the bivouac without any apparent detriment to health. Furthermore, the large size of the main tracheal vessels of the abdomen and the extensive ramifications of these vessels among the reproductive and other visceral organs indicates that the queen is well equipped in this respect to meet the crucial demands of a greatly increased metabolism during her brief gestational periods.

Although nothing is known concerning the Eciton queen's normal span of life with her colony, in all probability it is equal at least to one rainy season.   However, the hamatum queen for some reason is particularly short-lived after removal from the midst of her colony.   Three of our 13 contracted specimens lived only two days and only one lived longer than seven days in captivity after capture (see Table I).   As a control, one queen (1938 B) was permitted to remain with her colony for more than two weeks in the laboratory, then was removed (without anæsthesis) in good condition, yet this queen died within four days after she was segregated with a small group of workers.   Removal from the colony thus seems to introduce some change which makes inevitable the early death of captive Eciton queens.   Although in this study various preliminary attempts were made to discover the nature of the lethal factor, the results were not sufficiently clear to warrant discussion here.[8]   Whatever this factor may be,

[8] A possibility worth testing is that the Eciton queen when isolated from the mass of her colony is deprived of some essential food substance.   For instance, Zahl (1939) has found that workers and queens of the tropical ponerine ant *Dinoponera grandis* sicken and die after a few weeks in captivity unless a larval brood is present in the colony.

it appears to be specific for queens and not for workers, since in all cases workers remained alive in captivity for weeks after their queens had died.

From the above description of workers' responses to the queen during the bivouac-change movement, it is apparent that she must exert a powerfully attractive stimulative effect upon them. The basis appears to be mainly chemical. Even to the human observer the queen is distinguished by a delicate, fragrant odor, quite unlike the heavy, somewhat fœtid odor characteristic of Eciton workers. Workers are especially attracted to pieces of cardboard formerly in use as floors for the queen's cell, and will collect in the one of two compartments in which a queen has rested for a time. In artificial nests they gather about her, and follow closely as she runs about. When she comes to rest they pile the brood around her, and spend much time licking her and stroking her with antennæ. Our queens, placed in small wire cells at the top of the large cylindrical nests in which their respective colonies were clustered, were visited by large numbers of minim workers which penetrated the fine screening and remained to cluster in the cell. Thus the queen may be considered a factor of some importance in normal trophallaxis (Wheeler, 1928), the stimulative interrelationship of individuals which provides the basis for social organization.[9]

Characteristics and behavior of the physogastric queen.—At the time this study began a number of queens of *Eciton s. str.* species had been captured in various parts of Central and South America: notably *E. burchelli* by Wheeler (1921) in British Guiana, *E. vagans* by Gaige in Colombia (Wheeler, 1921), *E. hamatum* by Wheeler (1925), and *E. lucanoides* and *E. mattogros-*

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[9] However, it is doubtful that the workers in general are widely sensitive to the actual presence or absence of the queen as Wheeler (1921) implies they were in the case of a colony of *E. burchelli* from which the queen was removed. "I infer," he says, "that this was the only remaining female in the colony, for after her removal a perceptible apathy or dejection seemed to fall on the whole body of ants" (p. 298). Actually, this effect of "apathy," specifically a rather abrupt drop in general activity, characteristically ensues after large numbers of the ants have been stirred up and then permitted to recluster. Once reclustered, they fall into a lethargic condition whether or not the queen has been removed, hence this behavior cannot be attributed to a removal of the queen.

sense by Reichensperger (1926, 1934) and *E. quadriglume* and *E. rogeri* in the Argentine by correspondents of Carlos Bruch (1934). Thus by 1934 the queens of nearly all of the species of *Eciton sensu stricto* had been taken. It is interesting to note that in all of these cases the queen's gaster was contracted, a circumstance which led various writers (*e.g.*, Bruch, 1934) to conclude that the queen in question was "young," or "virgin."

The experience of the present writer was similar in capturing *Eciton s. str.* queens in Panama for behavior studies. In 1933 two queens, *E. hamatum* and *E. burchelli,* were taken; in 1936 four queens, one of *E. lucanoides* and three of *E. hamatum,* and in 1938 nine more of the last species, all of them alike in the fully contracted condition (see Table I). From these and other facts it becomes apparent that few if any of the queens of *Eciton s. str.* reported in the literature could have been virgin when captured,[10] and that the dichthadiigyne must be capable of returning to the contracted state after having delivered eggs. This interpretation in fact was offered as one alternative by Wheeler (1925) in reporting the first capture of the queen of *E. hamatum.*

Early in the present investigation, evidence concerning periodic changes in colony behavior, together with the experience of capturing numerous queens singly from colonies with broods in all stages of development, strongly indicated that the queen must pass repeatedly from the contracted to the physogastric condition, remaining in the latter condition only briefly before returning to the contracted state. Finally it became clear circumstantially that the eggs of a given brood must be laid during a short period of a few days near the end of the first week of the statary phase in colony behavior, when the colony is non-migratory.

Following this conclusion, in 1938 an effort was made to capture a hamatum colony at the critical time, which on circumstantial grounds was placed about seven days after the beginning of the statary period. On July 21 a colony (record number *38 H*) was found which although nomadic at the time was evidently nearing the statary phase, judging from the fact that its larval

[10] Probable exceptions are the two queens of *E. burchelli* taken by Wheeler and Emerson at Kartabo, British Guiana, in 1920 (Wheeler, 1921), in which circumstances point to the recent emergence of at least one and perhaps both of them from cocoons.

brood seemed very advanced and about ready to spin cocoons. After three further bivouac-change movements on successive days, when spinning appeared to be mainly finished in the brood, the colony settled down at a spot near station 4, Barbour trail.[11]

The statary bivouac was formed in a deep cranny near one end of a decayed fallen tree-trunk. The cluster formed a long elliptical curtain-mass filling the opening of the niche. On each of the following days, when the colony was revisited, the ants had only one raiding-system, a typical sign of the statary condition. The site was revisited on July 30, *i.e.,* one week after the beginning of the statary period, with materials for capturing the colony.

The colony had withdrawn about 30 cm. farther into the recess, very probably in response to frequent spattering by rain. Fortunately it was still fairly accessible. The bivouac was quiet, its forward wall sprinkled with ants holding cocoons in their mandibles. A dampened sheet was fastened securely across the opening to entrap the ants, then was sprinkled with ether. After four minutes, when the covering was removed, the major portion of the colony, a mingled heap of ants and cocoons on the floor of the cavity, was quickly scooped into a large jar. A few strands of ants still hanging, together with masses of eggs and clusters of small workers from the rear of the bivouac, were put into a second jar. In examining the material promptly after returning to the laboratory the first jar was found to contain the major part of the large enclosed pupal brood as well as most of the worker population. In the second jar, which contained workers and egg masses from the rear strands of the bivouac, a *physogastric queen* (Fig. 1) presently was brought to light in the part of the mass where workers minor and eggs were most numerous. Judging by relative positions in the jar, this queen must have occupied a position near the back of the cluster, probably among the hanging strands which contained most of the workers minor and most of the eggs. A careful inspection of the material revealed no other queens, no males, and two broods—a large enclosed pupal brood and an enormous clutch of recently delivered eggs.

Within the following twenty-four hours, which proved to be the

[11] The queen was seen in the procession during the final bivouac-change movement, and was judged to be in the contracted condition at that time.

span of life remaining to the *38 H* dichthadiigyne, her behavior was studied as continuously as other duties permitted.—

A few minutes after she was removed from the jar (4: 30 P.M., one hour after capture) the queen appeared to be recovering from anæsthesis, as indicated by reflex twitchings of tarsi and antennæ, although most of the workers remained immobile. At 4: 45 P.M. she had recovered sufficiently to gain an upright posture and had laid 20 eggs. At 5: 10 P.M. she was running about the Petri dish in which she had been placed, despite the trammeling effects of her huge distended gaster which tilted to one side or the other as she moved. From rough measurements at that time, her gaster was 16.5 mm. in length.

Until 8: 15 P.M. the queen remained undisturbed in a darkened Petri dish, laying more than 300 eggs. Then for an hour she was exposed at intervals to brilliant photoflood light when motion pictures were taken. Despite evident disturbance from the light, marked by shock reactions when light was introduced and by turning from the source, there was a describable regularity about the queen's behavior during this interval. There were successive periods of a few minutes each in which the queen stood in place, observably engaged in egg-laying, with intermittent periods in which she ran about the dish more or less continuously, dragging or carrying numerous workers on her gaster and followed closely by others. At no time was she moved by the workers, although generally a number of them remained close to her whether or not she was in motion.

The following representative notes were taken during two of the quiescent intervals, the first lasting 5 minutes after 9: 37 P.M. and the second 2 minutes after 9: 44 P.M.:

The queen abruptly breaks pace and suddenly stops in place, headed away from the photoflood source. She stands firmly on all six legs, with the ventral surface of the gaster resting on the floor. In oviposition, the eggs emerge in a wide jet from the vaginal orifice, and spread out radially upon the hypogynium. The process is marked by slight laterad oscillations of the the gaster and a shivering of the body and legs, which cease when eggs no longer emerge.—Eggs were laid during both of these halts.

At 11: 30 P.M. the queen with 6 workers was placed in dim light for observation. During the next 90 minutes there were 11 quiescent periods, varying between 30 sec. and 11 min. in duration (6 of them lasting between 1 and 4 min.). The intervening periods of activity were shorter, most of them around 3 min. in duration. In each case, locomotion began rather abruptly. The quiescent periods likewise began abruptly, with the queen usually sprawling close to the floor at once. Generally she stopped in a position facing away from the light, which although dim was sufficient to orient her. In some of the shorter intervals no eggs were laid. In the course of one or two of the longest stops, the queen shifted position briefly or moved forward a short distance once during the interval. The workers remained close to her, frequently applying their mouth parts to her body at the vaginal orifice and

at the surface of the hypogynium and licking these surfaces. After one of the stops a drop of viscous greenish-yellow fluid remained where the tip of the queen's gaster had rested. The workers soon found this drop and applied their mouth parts to it, evidently feeding.—Observations were discontinued at 1: 30 A.M., since no eggs had been laid during the preceding 30 minutes.—Between 5: 10 P.M. and 12: 00 A.M., 1245 eggs were laid.

In the morning, at 6: 30 A.M., only 358 eggs were found to have been laid during the night (*i.e.*, after 1: 30 A.M.). As before, alternating periods of quiescence and of activity were observed. Between 8: 15 and 9: 54 A.M. the queen was shielded by a ruby-glass filter and remained under observation. During this interval there were sixteen quiescent periods alternating with intervals of continuous locomotion, virtually all of the phases of quiescence and of activity falling between 1 and 4 min. in duration. In some of the stops between 20 and 30 eggs were laid, in others no eggs. The following notes typify egg-laying behavior:

8: 23 to 8: 26 A.M.—The queen stops abruptly, facing away from the weak light. Promptly there begins a shivering movement of the gaster, increasing at times to an oscillatory movement; then the oscillation becomes continuous, at times reaching 1 mm. in amplitude. These oscillations of the gaster begin locally and increase in amplitude, meanwhile spreading to include the entire body with the legs participating. Near the height of such spasms the eggs begin to appear. A jet of eggs between 12 and 15 units wide is forced slowly from the vagina directly backward over the hypogynium, with the eggs fanning radially to each side as they emerge. The eggs in small packets are either picked off by the workers or drop to the floor when the queen moves away.—Finally the queen breaks abruptly into motion, in an interval of locomotion which lasts 4 minutes in this case.

At 4: 15 P.M. the queen seemed less energetic than in the morning, and had laid only about 60 eggs since 10: 00 A.M. For about 20 minutes she was exposed to bright sunlight while photographs were taken, and although she was shaded between exposures the intense light appeared to exert a decidedly injurious effect upon her. At length she fell upon one side with flexed legs, unable to regain an upright position. At 6: 00 P.M. there were unmistakable signs of approaching death, which in the contracted queen is characterized by intermittent struggling and by local tarsal and antennal reflexes lasting a number of hours.—At 6: 30 P.M. she was chloroformed for fixation in Carnoy's solution and eventual preservation in 70% alcohol.

Notwithstanding the fact that disturbances incident to laboratory captivity must have disrupted the normal oviposition mechanism greatly, and although the factors which characteristically hasten death in captive Eciton queens must have been at work, certain inferences concerning the normal circumstances of physogastric function may be drawn from these observations. Concerning the queen herself, the regular occurrence of short

intervals of action and of quiescence (and egg-laying) in alternation indicates that a rhythmic process underlies the delivery of eggs from the ovarioles.   The abrupt onset of each quiescent period together with the oscillatory movements of the gaster and at times the entire body during oviposition speak for the operation of a fairly distinct egg-laying process arising at short intervals.   Likewise, the abruptness with which the queen broke into motion after each quiescent period indicates the regular recurrence of a rhythmic change in this process, evidently a phase during which more eggs became viscerally available for delivery.

Under the conditions of these observations the queen was attended by only a few workers, and space permitted her to run about in the intervals between egg-laying stops.   It is probable that under normal conditions in the bivouac, when she is surrounded by masses of workers, free locomotion is out of the question for the queen.   In that situation her viscerally-stimulated overt activity must be reduced to stirring in place and to interstimulative relations with workers.

This queen died with a considerable portion of her eggs still undelivered, a fact which together with other circumstances indicates that in all probability lethal processes setting in with captivity impaired the egg-production rhythm seriously from the beginning.   Under normal conditions in the bivouac this rhythm presumably functions smoothly and continuously throughout the period of approximately four days in which all of a given clutch of eggs is delivered.   Then, as we shall see, circumstances are such that the queen, contracted once more but in an exhausted condition, may profit by a long interval of recuperation before the parturitive ordeal must be repeated.

Our results shed some light upon the behavioral relation of the physogastric queen to her colony.   First of all, the fact that the queen is quite capable of locomotion during her time of physogastry effectively negates the hypothesis (Müller, 1886) that the colony must remain in place at such times because of an inability to drag along the heavy egg-laden queen.   She moves readily, and even drags or carries workers about with her, hence there is reason to believe that she would be quite capable of joining a bivouac-change movement if one happened to get under way.   She would

have to make periodic (viscerally enforced) stops on the trail, but could make the trek even though it might well be fatal.   We shall find that the sessile (*i.e.*, statary) status of the colony when the queen is laying her eggs is indeed related to the queen's oviposition cycle, but very indirectly, and very differently than the above hypothesis would suggest.

Our observations indicate that the normal stimulative attractiveness of the queen for the workers (*i.e.*, her trophallactic relationship with workers) is considerably increased during the time of oviposition.   The intersegmental membranes of her enormously swollen gaster and the hypogynium and vaginal regions in particular are highly effective centers of attraction.   The workers are constantly crawling upon her and licking these regions as well as the eggs when they appear (*cf.* Wheeler, 1900) and the (evidently much relished) small drops of fecal material which issue at times after egg-depositing episodes.[12]

There can be little question that this queen produced all of the eggs taken with the colony, a total of 17,062, which was estimated to be two or three thousand short of the actual number laid prior to capture.   To this we may add 2,046 eggs laid while the queen was held captive, and 7,190 unlaid eggs taken from her gaster in post-mortem study.   The total of 26,298 eggs approaches fairly close to the size of Eciton brood populations for which census studies have been made in other cases, offering further evidence that one individual dichthadiigyne is capable of delivering single broods of that size.   In view of circumstances indicating that the eggs of each huge brood are laid within a short interval of probably no more than three or four days, the entire performance seems quite worthy of being termed a stupendous feat.

The great susceptibility to death of the Eciton queen in this condition is attested by the fact that our specimen survived only about 30 hours after capture.   It is probable of course that her demise was hastened by the anæsthesis and by other shock-effects (*e.g.*, from intense light during photography), yet the fact that *contracted* queens similarly treated usually remain alive for as long as a week in captivity speaks for a specific physiological vulnerability to non-optimal conditions in the *gravid* Eciton

[12] Emerson (1939) has reported a similar observation for queen-worker relationships during egg-laying in termites.

queen. It is a fact of great adaptive significance that during this biologically critical time the dichthadiigyne ordinarily is assured the essential optimal situation through the operation of intrinsic factors which render the colony sessile. No less remarkable is the fact that *the queen herself, through her peculiar reproductive properties, is indirectly the basic controller of this state of affairs.*

EVIDENCE FOR A FUNCTIONAL RELATIONSHIP BETWEEN BROOD AND COLONY

Significant periodic differences in colony behavior.—As the first step toward working out relationships between the queen and her colony, let us examine the general situation of the series of *E. hamatum* colonies from which queens were captured for this study (see Table I).

In their behavior twelve of the hamatum colonies (*i.e.,* colonies *33 A; 36 A, B, D*, and *G;* and *38 C, X, D, E, F, G*, and *I*) from which queens were taken conform to the pattern previously described as "nomadic" (Schneirla, 1938). On the other hand only three (*i.e.,* colonies *38 A, B*, and *H*) conform to the pattern described as "statary." Since all of these colonies were studied for at least three days prior to capture, and some of them for longer times, any important deviations should have become apparent; but in all cases there appeared very clearly the characteristics of one or the other of the described activity patterns.

In cases showing the *nomadic* pattern, all of the colonies were *migratory,* that is, they had all engaged in bivouac-change movements near the end of each day in the period preceding capture. Without exception among many observations, the raiding activities of a given day *were terminated* by a complete movement of the colony, generally during the evening and early night, so that the next day found the colony developing a new raid from a different site generally more than 100 meters removed from the last.

Although their bivouacs were situated in rather different topographical circumstances, the clusters of the "nomadic" colonies were not secluded as is typical of statary colonies. The former almost without exception established themselves beneath logs, under matted vines, or against the sides of trees between buttressed roots, seldom within cavities such as hollow logs or trees. As a rule the larger portion of the more or less cylindrical mass

TABLE I

DATA RELEVANT TO THE 15 QUEENS OF *E. hamatum* CAPTURED IN THE PRESENT STUDY, AND TO THE COLONIES FROM WHICH THESE QUEENS WERE TAKEN (*cf.* FIG. 2)

Colony	Date (when queen captured; brood sampled)	Condition of queen, and span of life in captivity	Brood or broods			Colony behavior
			Eggs*	Larvæ*	Pupæ	
1933A	6/16/33	Contracted		Early stage		Nomadic
1936A	9/14/36	Contracted (6 da.)		Early stage	(Callows)	Newly nomadic
B	8/ 8/36	Contracted (3 da.)		Early	(Callows)	Newly nomadic
D	9/ 8/36	Contracted (4 da.)		Nearly mature		Nomadic
G	9/12/36	Contracted (7 da.)		Advanced		Nomadic
1938A	6/11/38	Contracted (7 da.)		$R = 0.36–0.73$ mm. $M = 0.46$ mm.	Advanced	*Statary*
B	6/15/38	Contracted (3 da.)		$R = 0.40–0.66$ mm. $M = 0.51$ mm.	Advanced	*Statary*
C	6/19/38	Contracted (3 da.)		$R = 0.35–2.0$ mm. $M = 0.75$ mm.		Newly nomadic
D	6/22/38	Contracted (10 da.)		$R = 0.44–3.68$ mm. $M = 1.23$ mm.		Nomadic
E	6/28/38	Contracted (7 da.)		$R = 0.35–4.20$ mm. $M = 1.8$ mm.		Nomadic
F	6/30/38	Contracted (4 da.)		$R = 0.60–4.35$ mm. $M = 1.76$ mm.		Nomadic
G	7/12/38	Contracted (6 da.)		$R = 2.10–6.58$ mm. $M = 3.32$ mm.		Nomadic
X	6/28/38	Contracted (2 da.)		$R = 0.36–0.73$ mm. $M = 0.47$ mm.	Callows	Nomadic
H	7/30/38	*Physogastric* (30 hr.)	$R = 0.26–0.58$ mm. $M = 0.47$ mm.		Early pupal	*Statary*
J	8/ 8/38	Contracted (returned to colony after 12 hr.)		Very young larvæ		Nomadic

* The growth stage of the respective broods taken in 1938 is represented by data on the range (R) and the mean (M) of body lengths (samples ranged between 25 and 200 specimens from each colony). The writer wishes to express his thanks to Miss Ruth Greene, who generously contributed her time to gather these data.

The larvæ of various *Eciton* species have been described by G. C. Wheeler (1943) with a key for their identification.

of ants was fairly exposed to view. It is typical that the bivouacs of nomadic colonies are far more readily approached and observed than are those of statary colonies.

In their raiding, particularly, colonies in the two behavior conditions exhibited very different characteristics. In the nomadic condition the Ecitons always staged vigorous daily raids which began promptly with the first daylight and grew rapidly into the characteristic maximal raiding pattern of the species. In *E. hamatum* this is marked by the growth of two or three (generally three) principal raiding systems, each a tree-like pattern of trails with a single principal trail as its line of communication with the bivouac. Although of course the details of the trail systems vary considerably according to the situation of the bivouac and the general topography, invariably multiple trail-systems are found under nomadic conditions. At such times a maximal number of ants from the population is drawn into the daily foray, developing extensive and complexly branched trails on a widespread front of raiding. With the raid probing out along a number of principal lines, the usual result is that roughly three-fourths of the circular zone around the bivouac is invaded, with the consequence that relatively enormous quantities of booty (mainly the soft-bodied young of other insects) are gathered in. *While nomadic, a colony remains near its peak of vigor in raiding and in other activities.*

With those colonies in the statary condition when their queens were captured the case was quite different in all important respects concerning behavior. Colonies *38 A, B,* and *H* were all known to have remained in their same bivouacs at least three days prior to capture. Colony *H,* for example, after three observed daily bivouac-changes, clustered within a large crevice in the side of a massive log on July 22, 1938, and was found in the same place and in almost the same spot on July 30, when captured.

Other evidence has been offered (Schneirla, 1933, 1940) for the existence of the statary period as a distinctive ''sessile'' phase of Eciton life. Observations on particular colonies extending over considerable periods have shown that once a hamatum colony enters a statary phase, it remains bivouacked in the same place

and exhibits other characteristic "statary" features of behavior during a period of approximately 19 days, before a major change occurs.

The fact will be recalled that of the fourteen colonies from which queens were captured in this study, only three were taken in the statary condition. This difference is scarcely a matter of accident, but is due to the relatively secluded locations taken by colonies of *Eciton s. str.* when they are statary. Colony *38 H*, clustered in a deep crevice on the outer wall of a huge log, was unusually accessible for a statary colony. The virtual impregnability of statary colonies is attributable to two facts in particular. First, they are commonly clustered within a cavity, generally in a hollow log or tree. Colony *38 A* had to be extracted from a hollow log, colony *38 B* from within the large hollow root of a standing tree, by drilling a circle of holes with brace and bit and breaking out an opening through which the ants could be removed by hand.[13] Then, too, if a statary colony happens to settle where it is somewhat exposed to the elements, disturbance from wind, rain or sunlight causes the ants to shift their position so that after a few days capturing them would require the assistance of a wrecking crew. The proneness of colonies to cluster in hollow logs or trees when entering the statary period stands as a highly adaptive circumstance for which no specific explanation can be advanced at the present time.

Without exception, each of our three statary colonies from which queens were obtained had a single raiding system when captured. This pattern is readily recognized by the presence of just one principal raiding trail leading from the bivouac, rather than two or three as in the nomadic phase. Distance reached from the bivouac in the raiding is not a secure criterion of its relative vigor, since in the statary phase the chemically-marked route of a previously used trail may be employed on more than one day so that such trails often become greatly extended beyond the distances ordinarily reached in nomadic-phase raiding. As more certain indications of reduced raiding, the number of principal systems is one rather than three, and there is a smaller

[13] Dr. Neal Weber kindly assisted in this operation, which was completed in a torrential rain.

number of branch trails in that system than is characteristic of
a raiding system in the nomadic phase. Thus, *in the statary
phase, raiding activity falls much below the level of vigor and of
numbers involved during the nomadic phase.*

Before considering the relationship of these periodic differences
in Eciton behavior, it is desirable to examine correlated differ-
ences in the internal constitution of the colony.

Intrinsic conditions underlying colony behavior.—A considera-
tion of the internal characteristics of the colonies (see Table I)
shows that the external behavior differences were paralleled by
others no less outstanding. The intrinsic differences may be
represented by a comparison of the two groups of colonies in
terms of their condition and the status of their brood or broods
when the queens were captured.

First of all, it should be emphasized that the broods invariably
were *worker broods,* and that no batch of larvæ or pupæ con-
tained individuals departing sufficiently from the others in form
or size to suggest the anlagen of fertile forms. This statement
is of course not based upon our present facts alone, but finds its
main support in an examination of hundreds of Eciton broods
on Barro Colorado Island in *rainy months* between May 15 and
September 20 in four different years which has disclosed none
but worker forms in them.

Another fact of significance is that while each of the broods
contained tens of thousands of individuals, all members of a given
brood were *roughly at the same stage of development.* This con-
dition held not only when a single brood in the larval stage was
present, but also for cases in which there were two broods (*i.e.,*
a pupal brood in addition to a brood in the very early larval
condition). This statement, likewise, is based not only upon the
present data but also upon the invariable finding that in *E.
hamatum* the entire population of a given mature larval brood
terminates that stage and spins cocoons within a very few days,
and that pupal broods mature and are removed from their cocoons
as callows within a similarly short period of three or four days.

All three of our statary colonies had two broods at well-sepa-
rated points of development, a fact which we shall find character-
istic of the *latter* part of this activity phase. Colony *38 H* con-

tained a well-advanced pupal brood as well as a massive batch of newly laid eggs. Colony *38 A* contained a still more advanced pupal brood, and its younger brood had largely hatched and passed into the early larval period. The two broods of colony *38 B* corresponded in general to those of *38 A*. In the early days of the statary period only one brood (always a pupal brood) is present.

In contrast, the nomadic colonies each contained only a single brood, in every case *in the larval condition.* From the size data on these broods, represented in Table I by the averages and ranges of individual body lengths, it is apparent that the broods were at very different stages of development when the colonies were captured. If a greater magnitude of body length in the brood (as indicated by larger averages and greater ranges) may be taken as valid evidence for an advanced point in growth, the nomadic colonies captured in 1938 may be placed in the following sequence: *X, C, D, E, F* and *G*. It will be noticed that with the single exception of colony *X*, there is a correspondence between the chronological order of capture and the growth point attained by the respective broods. The possible significance of this fact will be considered in a later connection.

When we bring together our facts concerning the external and internal characteristics of the colony, a significant parallelism is evident between them for both the nomadic and the statary phases. In the statary phase 1) the colony does not migrate but remains in a given place, 2) by virtue of its secluded location it is well protected from the elements and from animals, 3) it raids minimally and is comparatively lethargic, and 4) it contains a pupal brood and in its latter part (*e.g.,* colonies *38 A, B,* and *H*) eggs or a young larval brood as well. *The most significant parallel circumstances are a low condition of colony activity and a brood (or broods) incapable of overt activity.*

In sharp contrast to the above situation, a colony in the nomadic phase 1) regularly moves to a new bivouacking site at the end of each raiding day, 2) generally bivouacs in fairly open places, 3) raids maximally and appears to be always (*i.e.,* in the daytime) near the peak of activity, and 4) contains a single brood in a more or less advanced larval phase. In this case, *the*

*most significant parallel circumstances are a high point in colony
activity and the presence of a larval brood which is capable of
overt activity.*

*Theoretical explanation of the parallelism between brood con-
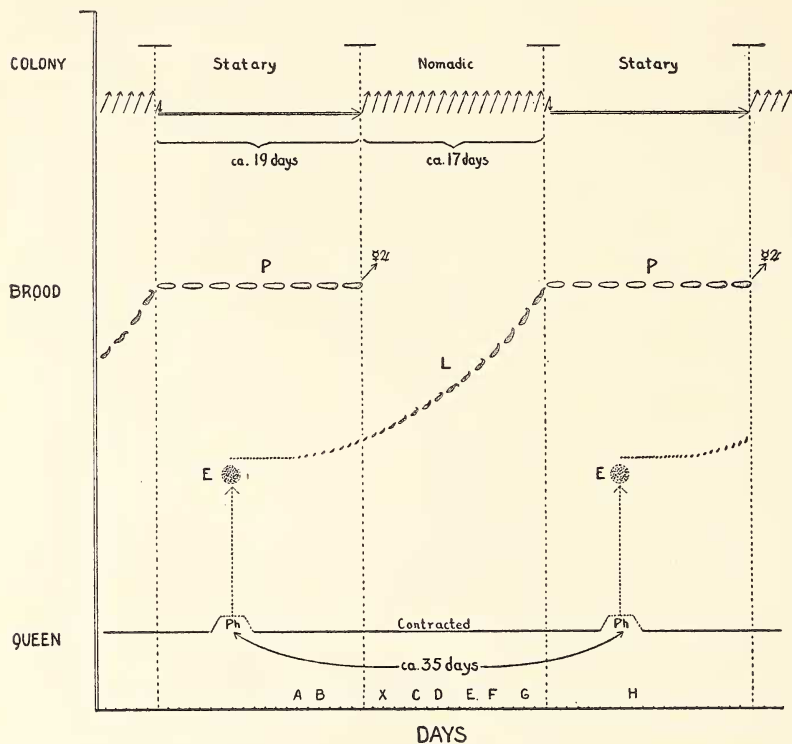dition and colony behavior.*—These facts suggest that a causal

FIG. 2. Schema to represent concurrent events in *colony behavior* (top),
condition of the brood, and *function of the queen* in *E. hamatum.* (The
sequence of given events in the colony may be traced horizontally, the con-
currence of events, vertically.) *A–H*, approximate situation of the respec-
tive colonies from which queens were captured in 1938; *Ph*, physogastric
interval of the queen; *E*, egg mass delivered in given physogastric interval;
L, larval stage of brood; *P*, pupal stage of brood; ☿ ♃, workers minor and
major of a callow brood.

relationship exists between the condition of the brood and the
circumstances of general activity in the colony. The conclusion
appears justified that conditions arising from the capacity of the

brood for overt activity somehow account for the critical difference which appears in general colony activity pattern when active broods rather than ''passive'' broods are present. This idea has been advanced in a previous connection (Schneirla, 1938) and will be carried further presently.

Evidence from field observation and special test supports this inference of a causal relationship dependent upon condition of the brood. Batches of eggs and very young larval broods (as in the statary colonies *38 A, B,* and *H*) are as a rule gathered into a single mass or a few masses which are covered and at times permeated by minim workers and are only very indirectly in contact with the adult population of the colony. On the other hand, when the larvæ have developed further (as in colonies *38 C, D, E, F, G,* and *X*) and their twisting movements become perceptible to the unaided eye, these masses are broken up and more or less distributed through the bivouac, so that larval activity and other stimulative effects may directly reach large numbers of adult workers. When the larvæ mature, and become enclosed in cocoons, it is apparent that in the ensuing pupal stage (as in colonies *38 A, B,* and *H*) they become passive contents of the bivouac. Heaped in interior pockets of the cluster and held by workers distributed through its wall, they are presumably neutral in importance or may actually exert a quieting effect upon the workers that clutch them in their mandibles, somewhat as the pressure of thumb-in-mouth pacifies an infant.

From laboratory observations we may say that through the presence of an active larval brood the workers are distinctly stimulated so that the amount and the vigor of their activity increases greatly. When Ecitons are divided into part-colonies of comparable size, it is the groups with larvæ that show the greater activity both within the confines of their artificial nest and in the frequency of visits to an adjoining food-place, as compared with groups that have no brood or have a pupal brood in cocoons. When we study the relationships of individuals within the nest, there are clear indications that this difference in activity level actually depends upon a stimulative effect from the larval brood. Typically the larval brood is spread over an area, usually around the queen if one is present. The workers move restlessly around,

frequently touching the larvæ with mouth-parts or licking them, intermittently touching and stroking them with antennæ, often picking them up and shifting their position slightly or carrying them bodily from place to place.   When pieces of food are carried into the innermost nest area, they are commonly deposited near the larvæ or actually laid upon them, so that in their almost incessant twisting movements the larvæ readily bring their mouth parts into contact with the food.[14]   It is a common observation that stimulation from passing workers may arouse quiescent larvæ to squirming activity, or that chance stimulation from larvæ may bestir workers.   It is manifest that the larvæ thus in a number of ways arouse the adults to increased activity, in the mutual stimulative relationship between adults and brood which Wheeler (1928) has termed ''trophallaxis.''[15]

On the other hand a group without any brood or with pupæ in cocoons is distinctly less lively than when larvæ are present. Even when exposed to light the workers seldom appear very excited, and most of the time they stand quietly over their heap of cocoons or near it, or move slowly about in the vicinity.   Under these conditions Ecitons are chronically less feverish in their activity, indulge in many fewer excursions from the nest, and hence they carry in far less food than in the larva-containing situation. We may say that *the group or colony which contains active larvæ as in the nomadic period has a special source of colony ''drive.''* In contrast, in the statary period, this factor is greatly reduced when interindividual stimulation is limited to relationships among adult workers themselves.[16]

[14] Gallardo (1920) has commented upon the great mobility of Eciton larvæ.

[15] The gastric anatomy of the larvæ of *E. burchelli* and the feeding behavior of these larvæ have been described by Wheeler and Bailey (1920). In this species the larva is fed at frequent intervals on boluses composed of the soft parts of insect prey, laid by the workers upon the ventrum of the larva or actually thrust into the larval gullet.

[16] From his observations on a colony of *E. burchelli*, Wm. Müller (1886) inferred that an increase or decrease in the raiding activities of a colony is attributable to the relative need of the brood for food.

''Larven brauchen ja im allgemeinen, besonders kurze Zeit vor der Verpuppung, bedeutend mehr Nahrung als die fertigen Insekten, und so scheint nichts natürlicher, als dass das Nahrungsbedürfnis der

However, in a statary colony with advanced pupæ there is a marked change in the general level of activity when the nearly mature individuals begin to move within their cocoons. When a close approach to the end-point of pupal development is indicated by the appearance of a distinct pigmentation of eyes, mandibles, and anterior sections of the body, activities such as twitchings of the legs and slight turnings of the body become observable. Such movements of the pupæ may be increased by picking individuals up with tweezers or by lightly probing the body, just as they are perceptibly elicited when the cocoons are picked up by workers. The stirring of mature pupæ appears to excite the workers and evidently leads to the removal of the brood from cocoons; the envelopes readily tearing open as the workers manhandle them (Schneirla, 1934, pp. 320–321). That the opening of cocoons depends critically upon pupal movements is suggested by the fact that test groups did not open cocoons in which the advanced pupæ had been killed with a needle (*op. cit.*, 1938, p. 66).

There is a distinct increase of excitement in an Eciton colony as emergence of its brood gets under way. The excitement rises in crescendo until, a day or two later when the largest part of the brood is free and active as callow individuals, the colony shakes itself from the statary period by staging an exceptionally vigorous raid *ending in a bivouac-change movement.* Laboratory observations show that in the appearance of a new pupal brood and in the strong stimulative effects from callows during their first few days as ''free'' individuals in the colony, an Eciton worker population receives a great lift in internal ''drive.'' The conclusion seems in order that this internal change is responsible for setting a colony into the nomadic phase.

Gesellschaft ein geringeres wird und die Tiere entsprechend weniger auf Beute ausgehen, nachdem alle Larven eingesponnen '' (p. 87). While this point undoubtedly has relevance to the *phylogenetic* problem (concerning the evolution of the Eciton behavior pattern) and describes an important adaptive function of the pattern, it is teleological and misleading if applied to the *ontogenetic* problem (concerning the contemporary causation of the pattern in a given colony). As the present discussion shows, it is not the brood's food-consuming capacity as such, but the presence or absence of incidental tactuo-chemical stimulation from the brood which critically governs periodic changes in colony behavior.

Our theory thus accounts for the nomadic-statary (rainy-season) cycle of Eciton colony activity in terms of cyclical changes in the internal stimulative properties of different broods. In Figure 2 the relationship is represented schematically in terms of a diphasic diagram, on which are indicated the positions evidently attained by our colonies at the times their respective queens and broods were captured. The "trough" phase of the cycle signifies the statary period, in which the colony is held in position and is comparatively inactive and the brood or broods relatively passive in their social rôles. A colony enters this statary phase when the enclosure of its mature larval brood removes the major internal source of special social stimulation. The appearance of a new brood as eggs laid after about one-third of the period has elapsed does not materially change general colony behavior, since with this brood concentrated in masses, incapable of movement, it can exert only a relatively negligible stimulative effect upon the general population. As a matter of fact, the vigor of raiding seems to decrease somewhat toward the middle of the statary period, and hamatum colonies sometimes show raidless days then (also *E. burchelli*, as Müller (1886) noticed). With social stimulation low throughout the period, the workers are only weakly stimulated to leave the colony in raiding, with the result that statary-period raids are relatively feeble as compared with nomadic-period raids.

We may say that in the statary period a low summation of colony excitement directly expresses its limitations in the underdevelopment of raiding, which roughly is only about one-third as extensive as in the nomadic period. Such raids may be regarded as underdeveloped not only in their restricted numbers and scope but also in falling below the threshold of development at which a bivouac-change movement becomes inevitable.

To speak of a "threshold" of raiding essential for new behavior requires us to show why underdeveloped raids cannot lead into a colony movement. This has been done in special studies of the relationship between raiding and the bivouac-change movement (Schneirla, 1938, 1944) which bring out the reason why a colony can withdraw to its original bivouac from an underdeveloped statary-period raid but must move onward when a maximal

nomadic-period raid has been staged. The actual behavior process, fairly complex, centers around the fact that in the statary period the colony is insufficiently rearoused (by regular post-meridional atmospheric changes) after the midday lull in activity, so that no exodus exists capable of blocking the principal trail to returning raiders. In the nomadic period, on the other hand, the afternoon rearousal produces a lasting afternoon exodus from the bivouac which forcibly reorients returning raiders outward in at least one trail system; then a movement from the bivouac persists on this route, eventually draining the entire colony to a new bivouacking site. Thus when extrinsic stimulation (from light in particular) drops away at dusk, a colony in the statary phase loses its principal source of arousal and gradually approaches quiescence; whereas a colony in the nomadic phase when raiding declines with dusk possesses an adequate and persistent internal ''drive'' facilitating the vigorous exodus already in progress. The key to the situation appears to be the radical difference in the intrinsic properties of colonies in these two conditions.

The break from the statary phase appears to be accomplished not through the influence of the new larval brood, which at that time seems insufficiently developed to be a social-stimulative factor of any account, but rather through activities centering around the maturation of the pupal brood and its appearance as an enormous horde of hyperactive, voracious callows. Invariably, hamatum colonies shift from their statary sites when the pupal brood has largely emerged; the deserted spot is littered with empty cocoons, and the first bivouac-change processions are distinguished by crowds of pale-colored callow workers. Circumstances indicate that the stimulative effect from tens of thousands of callows not only serves to bring the colony into nomadic life, but also persists for a few (apparently about five) days as a factor of similar influence and importance. Our colony *38 X* was taken at such a time. As a major source of stimulation, the presence of the callows appears to overlap the involvement of the new brood of larvæ, in that as the callows lose their early social-stimulative effect and merge into the adult worker population, the larvæ become increasingly functional in this respect. About five

days after the nomadic period has begun, typically, the callows are almost indistinguishable from regular workers and (judging from laboratory observations) have dropped to the level of the ordinary workers in their trophallactic properties. Meanwhile, the larvæ have increased notably in size and activity, most of them are capable of feeding, and at this time they appear to constitute the new major source of social stimulation or intrinsic colony "drive." Our colony *38 C* was taken at such a time. When it was captured, the larval brood was distributed rather widely through the interior of the bivouac, and in the laboratory a pronounced activity was noted in all but the smallest size category.

Colonies *38 C, D, E, F,* and *G* (taken in chronological sequence) may be placed at successive points in the nomadic period on the basis of the invariable fact that an increasing development of the larval brood parallels an advance through this phase of activity (see Fig. 2). Not only are the trophallactic properties of the brood instrumental in maintaining the nomadic pattern of behavior by supporting daily maximal raids, but as the larvæ develop further their influence appears to increase. The apparent augmentation of their social effect probably is due to increased chemo-stimulative properties as well as to greater general activity as they grow. This is suggested by laboratory observations and by the fact that in the bivouac more advanced broods tend to be widely distributed through the cluster, single larvæ held by individual workers much more frequently than with younger broods. Thus the intrinsic "drive" effect of the brood not only maintains the nomadic pattern in the colony, so that maximal raids and bivouac-change movements appear regularly in the daily routine, but this relationship appears to rise through a crescendo as brood development nears its climax. Hence, near the end of the nomadic period, raids are more extensive and more heavily populated, and colony movements tend to carry over longer distances than earlier in the period. In particular, this is revealed by studies of individual colonies throughout the nomadic period (*e.g.*, colony *1936 A*,—Schneirla, 1938; also *E. burchelli,* colony *38 I*,—Schneirla, 1944).

As we have pointed out, in addition to postulating an excitation to "maximal" raiding through the drive effect of active broods,

the theory postulates a given threshold in raiding which is essential for the occurrence of a bivouac-change. As the relationship has been worked out in a previous paper (*op. cit.*, 1938), only in the nomadic period does raiding attain the pattern (*i.e.*, three trail systems in *hamatum*) and the degree of colony involvement that is required if it is to eventuate in a colony movement. That the essential ''maximal'' pattern of activity in the colony depends specifically upon a characteristic larval-brood influence is suggested strikingly by the regularity with which colonies lapse into the statary period on the very day most of the larvæ have spun their cocoons.

It seems clear that since a critical difference in the pattern of hamatum colony behavior depends upon the condition of the brood, the ultimate determination of such matters resides in the individual that produces the broods, *i.e.*, the queen.

THE ECITON QUEEN AS PACEMAKER FOR COLONY BEHAVIOR

It is characteristic of *E. hamatum, E. burchelli,* and other representatively terrestrial species of *Eciton s. str.* (if not Ecitons generally), that broods appearing in the rainy season are very large, and that all individuals in a given brood develop concurrently. That is, in each new *hamatum* brood the eggs are laid within a span of a few days, pass through the larval period essentially in step, enter the pupal stage within about four days, and appear as callow workers all within a very short period. Obviously this state of affairs depends essentially upon the reproductive properties of the Eciton queen.

Let us first consider some further facts about brood development that throw light indirectly upon the capacities of the queen. Population studies have been made with four broods captured on Barro Colorado Island, with these results: *E. hamatum*—a larval brood, 26,452 individuals (not complete), a pupal brood, 31,379 individuals (fairly complete); *E. burchelli*—one complete larval brood of 36,888 individuals, and a pupal brood of 31,298 individuals. Then too, the mass of eggs from physogastric queen *38 H* totalled more than 26,000, probably with a few thousand missing. Since many other broods inspected in the egg, larval, or pupal condition were comparable in bulk with these populations

which were actually counted and sized, it seems that the rainy-season broods of *E. hamatum* (and of *Eciton s. str.* broadly) are typically very large. In all probability the broods in this season comprise more than 25,000 individuals as a rule. That a single queen is capable of delivering an egg mass of these proportions within a few days is an impressive fact.

Beyond the fact that in nearly twenty captures we have never found more than one queen in a colony, and the fact that the enormous clutch of eggs in colony *38 H* may be attributed safely to a single queen, our evidence on condition of the broods seems to exclude any possibility that more than one queen figures in producing a given brood. First of all, the range and central tendency of body size in young and advanced larval broods are rather constant for given stages (see Table I). The range of individual sizes is at first limited (*e.g.*, colonies *38 H, A, B,* and *X*) but increases with the general age of the brood (colonies *38 C, D, E, F, G,* and others). That there is a definite unimodality in the distribution of individual sizes within a given brood was indicated by study of the broods mentioned above, and has been verified in all four of the broods surveyed in toto. Furthermore, all brood distributions are skewed toward the worker-minor extreme. With the population classified into five body-size categories (in terms of body length), with No. 1 the smallest and No. 5 the largest, the mode falls in category No. 2 as a rule, well below the median value. For example, in a hamatum pupal brood (of 31,379 individuals in cocoons) which was surveyed, the following distribution was found through the five size categories, from smallest (ca. 5 mm. long) to largest (ca. 10.5 mm. long) : 5,209, 16,860, 8,072, 870, and 368, respectively. The prevalence of the described distribution pattern in Eciton brood populations indicates the involvement of a single reproductive source in each case, a maternal source having definite and regular properties.

As further evidence we may repeat the fact that enclosure of the larval brood and the opening of cocoons when a pupal brood hatches are matters of mass change, both events accompanied by prominent changes in colony behavior. In view of these considerations together with our invariable discovery of but one queen to a colony in many captures, the conclusion seems justified

that these large worker broods appearing in *hamatum* (and in
burchelli) colonies are attributable to single queens in the respec-
tive cases.[17]

Furthermore, the time relations of successive broods in given
colonies are sufficiently predictable to suggest the function of but
one queen in each case. The results from colony *36 A* (*E. ha-
matum*), which was studied during a period of 42 days, from
August 5 to September 15, 1936, bear directly on this point
(Schneirla, 1938). During seven weeks of observation, this
colony passed from a statary period into a nomadic period which
lasted 17 days, then spent 19 days in a new statary period, after
which it entered a further nomadic period. Three successive
broods were observed, all of them relatively immense and entirely
composed of worker forms. The first of these broods terminated
its development and appeared as callow workers when the study
began. The second brood was present as developing larvæ
through the complete nomadic period, was enclosed in cocoons
and entered the phase of pupation when the fully observed statary
period began, passed through its pupal development and ap-
peared as callows as a further nomadic period got under way.
The eggs of the third brood were laid at some time between Au-
gust 28 and September 6, and this brood was well started on its
larval development when the colony was captured September 15.
In the end the colony was anæsthetized and thoroughly examined.
Only one queen (in the contracted condition) was found.

This evidence is brought together in the schematic representa-
tion of the hamatum behavior cycle in Figure 2. The condition
of the brood or broods as indicated at times of major change in
colony behavior corresponds to the facts for colony *36 A* and
checks with many other cases, as does the representation of a
developing larval brood through the nomadic period and a pupal
brood through the statary period. Our records indicate that in
the area of this study individual hamatum (and burchelli) col-
onies characteristically pass through the cycle of correlated be-
havior changes and worker-brood production a number of times

[17] A possible alternative explanation is that the broods are the product of
two or more queens with exactly synchronized visceral rhythms. This seems
very doubtful, especially because no polygynous colonies have been dis-
covered.

in regular succession during the first four or five months of the rainy season.

To describe the characteristic time relations of the principal changes in brood development for *hamatum,* it is necessary to ascertain the time at which the eggs are laid more exactly than is possible from the record of colony *36 A.* From general evidence, and from the facts concerning queen *38 H,* we have inferred that the process of egg-laying occurs during a short period following about one week after the beginning of the statary period. The conclusion that normally a new brood appears as eggs about ten days before the end of each given statary period is supported directly and indirectly by numerous facts. In particular, although eggs are never found in colonies examined during the first few days of the statary period, large masses of eggs are found during the last week of this period. Queen *38 H* evidently had just passed the peak of an egg-laying process when captured seven days after the beginning of a statary period. Since in *hamatum* oviposition appears to be of short duration, probably no more than three or four days from beginning to end, if we set 18–20 days as the usual length of the statary period in this species we may say that the new brood has roughly ten days of early development before the statary period ends.

On this basis we may estimate the developmental period of a given brood. To the first 10 days of embryonic and early larval growth when the colony is statary, and 17 days to complete larval development in the nomadic period, we may add 19 days (as a close approximation) in the pupal stage during the following statary period. That makes a total of 46 days for the complete development of a hamatum brood. Other facts plainly indicate that the interval between the appearance of successive broods in a given colony is the number of days from the end of one statary period (when one brood is delivered as callows) to the end of the next statary period (when the next brood is delivered), *i.e.,* about 35 days.[18]

[18] As may be seen in Figure 2, the difference of about 10 days in the above figures is attributable to the fact that the oviposition and early development of a given new brood overlaps the period in which the preceding brood is completing its pupal maturation.

On this basis we may arrive at an approximation of the interval between successive occurrences of the short but strenuous oviposition act of the queen. After having deposited a given clutch of eggs, the queen evidently lays no more until the early part of the next statary period. If the peak of one process is roughly placed at seven days after the beginning of a statary period and its end at nine days, for the ensuing resting phase there are ten days remaining in the same period, 17 days in the ensuing nomadic period, and perhaps five days in the following statary period,—32 days in all for the interval between successive intervals of actual egg-laying. This checks fairly well with the figure offered above for the interval between the appearance of successive broods of callows, as it obviously should.

To repeat, there is every reason to believe that in a given hamatum colony the broods appearing at intervals of about 35 days are the progeny of a single queen. Not only the facts concerning the capture of queens, but also the highly predictable time relations between successive broods, support this conclusion. The facts as sketched in Figure 2 indicate that the entire set of events is highly synchronized; particularly in the ability of the queen to deliver a new batch of eggs about 12 days before the previous brood joins the worker population of the colony. The evidence suggests that in our area of study a given hamatum queen is capable of repeating this process a number of times during the first months of the rainy season and perhaps even longer.

Thus in an indirect manner but nevertheless very effectively the queen is the pace-setter of the cyclic changes which have been described for the type species. This relationship appears to hold for other *Eciton s. str.* species as well (*e.g., E. burchelli, E. vagans*), and perhaps also in other *Eciton* subgenera.

To summarize, in *hamatum* we seem to have the master pattern, as it were: 1) the queen at regular intervals and in a strikingly precise manner furnishes a huge mass of eggs which begin their development almost simultaneously, 2) the given brood does not materially influence events until the emergence of the previous brood as callows dynamizes the population into nomadism, 3) then the new brood (as larvæ) takes over as principal source of

the ''social stimulation'' which maintains the highly dynamic activity pattern of the colony for some time; 4) when the ''drive'' effect of the larval brood is removed as it enters the pupal condition the colony lapses into its minimal activity pattern, from which 5) the emergence of this brood as callow workers arouses it into a new dynamic phase—and so on.

The queen is the key of this entire process, but only in an indirect manner through her physiological properties as the producer of successive broods. After a given brood has appeared as eggs we may say hypothetically that the presence of the queen is essential neither for the next major change in colony behavior nor for the maintenance of this change (*i.e.*, for nomadism). In fact without the queen the next sessile phase of the colony-behavior cycle may also occur and the colony will even begin its next nomadic period (*cf.* Fig. 2). However, if no new brood is forthcoming we should expect the colony to lapse from its new nomadic phase into an aberrant and mainly sessile type of existence, *i.e.*, a protracted statary condition. Some evidence corroborating this prediction is in fact available from the study of colonies deprived of their broods.

To state the hypothesis in a different way, it is quite likely that in the dry season when Eciton broods are very small (either through metabolic insufficiency in the queen or through brood cannibalism in the workers, or both of these), the colonies lapse almost completely into statary life. But under optimal conditions in the rainy season, the adequate condition and regular labors of the queen periodically furnish the colony, in an incidental manner, with the changes in trophallaxis-based social stimulation which condition the drive (or lack of drive) underlying alternate changes in the general behavior cycle.

The exquisite synchronization of the set of relationships involved in the Eciton behavior pattern is emphasized in several ways when the queen is considered in her rôle of key individual. Through her capacity to deliver an entire batch of eggs within a few days, the queen indirectly contributes the precision with which the colony shifts from one mode of life to another. This in turn promotes a further characteristic of great adaptive value. Due to the spacing of her successive broods, the queen becomes

physogastric and lays her eggs *only at times when the colony happens to be statary* (see Fig. 2), a combination of events which is most opportune for survival of colony and species. It is apparent from our discussion of the indirect relations existing between the cycles of queen and colony functions that a true *convergence* of events occurs in this case, which serves to guard the queen from injury at the one time she is most vulnerable. When she is gravid, having to make her way over a long bivouac-change trek undoubtedly would offer a serious risk for the queen, carrying the constant threat of dangers such as a tumble from elevated sections of the path on vines or tearing the tightly stretched intersegmental membranes on rough surfaces. Instead, thanks indirectly to her own visceral regularity, the queen is safely immured through this critical period, and moreover, there follows a further time of safety during which she may convalesce from the organic ordeal of large-scale oviposition. Not least among the factors fitting into the marked adaptivity of this synchronized pattern of events, the bivouac of the colony in its statary phase is characteristically more sequestered than at other times. Altogether, it would be difficult to find a more effectively adaptive mosaic of various biological events than this one, based upon the physiological properties of the Eciton queen.

SUMMARY AND CONCLUSIONS

The functions of the *Eciton hamatum* queen serve indirectly as a pace-making factor in the colony behavior pattern of the species.

The determining processes in a given colony center around the reproductive properties of the single functional queen. Except when colony bivouac-change movements occur the fertile queen is confined to the bivouac, evidently to a large extent because of her pronounced photonegativity. At regular intervals of approximately 35 days the dichthadiigyne becomes physogastric and within a few days releases a mass of more than 20,000 eggs. Between egg-delivery episodes she remains in the contracted or ''resting'' condition. The ability of the hamatum queen to mature and deliver an immense number of eggs within a very limited time means that all members of a given brood develop

and mature roughly in synchronization. These facts hold important consequences for the colony behavior pattern.

In the rainy season of the Caribbean lower rain-forest zone of Panama, a colony of *E. hamatum* passes through statary (minimal raiding; absence of migration) and nomadic (maximal daily raiding; successive daily bivouac-changes) behavior phases at regular intervals, each period lasting nearly 20 days. Depending upon the properties of a fertile queen, the alternation of these behavioral phases is highly predictable.

Significantly different intracolony circumstances parallel the two phases of the colony behavior cycle. Colonies in the nomadic condition invariably contain a single brood passing through its larval stage, and the period ends precisely when this brood has become mature and is mainly enclosed in cocoons. In statary colonies a brood in the pupal stage is found, and the period ends when this brood has matured and has mainly emerged as callow workers. Approximately seven days after a given statary period has begun, a new brood of more than 20,000 eggs appears.

The intimate correspondence which exists between Eciton colony behavior and brood condition is explicable in terms of the Wheeler *trophallaxis* concept. Evidence is cited for the involvement of a special social-stimulative effect, a superadded ''drive'' factor, furnished by broods capable of extensive overt activity. Emanating from a newly emerged lot of callow workers, this effect arouses a previously sessile colony to the threshold of maximal raiding and daily bivouac-change, and thus is responsible for initiating a new nomadic period. Furthermore, due to a rather precise synchronization of successive broods, before the energizing function of a new callow brood runs its course it is overlapped and succeded by the similar function of a sufficiently developed larval brood. This larval effect maintains the nomadic condition over a considerable time, but the colony lapses promptly from nomadism when the larvæ mature and spin their cocoons. Thus the sessile and relatively inactive statary condition which ensues is attributable to the existence of an inadequate energization of the colony when the brood (eggs; pupæ) is incapable of functioning as an effective source of social stimulation.

Periodic changes characterizing Eciton colony behavior thus basically depend upon a highly regular reproductive cycle in the

queen. By furnishing new broods at fixed intervals, the queen's function indirectly governs the presence or absence of the intra-colony dynamizing factor critically responsible for the ebb and flow of events in the Eciton behavior pattern.

LITERATURE CITED

André, E. 1885. Species des Hyménoptères. (Supplement au species des Formicides d'Europe et des pays limitrophes.) 8: 838–840.

Bruch, C. 1934. Las formas femeninas de *Eciton* . . . Descripcion y re-descripcion de algunas especies de la Argentina. Ann. Soc. Cient. Argent., 118, 2nd sem., 1934: 113–135.

Emerson, A. E. 1939. Social organization and the superorganism. Amer. Midl. Nat., 21: 182–209.

Gallardo, A. 1920. Las hormigas de la República Argentina—Subfamilia dorilinas. Anal. Mus. Nac. Hist. Nat. Buenos Aires, 30: 281–410.

Müller, W. 1886. Beobachtungen an Wanderameisen (*Eciton hamatum* Fabr.).[19] Kosmos, 18: 81–93.

Reichensperger, A. 1926. Das ♀ von *Eciton mattogrossensis* Luederw. (Hym.) Ent. Mitteil., 15: 401–404.

———. 1934. Beitrag zur Kenntnis von *Eciton lucanoides* Em. Zool. Anz., 106: 240–245.

Schneirla, T. C. 1933. Studies on army ants in Panama. Jour. Comp. Psychol., 15: 267–299.

———. 1934. Raiding and other outstanding phenomena in the behavior of army ants. Proc. Nat. Acad. Sci., 20: 316–321.

———. 1938. A theory of army-ant behavior based upon the analysis of activities in a representative species. Jour. Comp. Psychol., 25: 51–90.

———. 1940. Further studies on the army-ant behavior pattern. Mass organization in the swarm-raiders. *Ibid.*, 29: 401–460.

———. 1944. Studies on the army-ant behavior pattern. Nomadism in the swarm-raider *Eciton burchelli*. Proc. Amer. Phil. Soc., Phila., 89 (1) (in press).

Weber, N. 1941. The rediscovery of the queen of *Eciton* (*Labidus*) *coecum* Latr. (Hym.: *Formicidæ*). Amer. Midl. Nat., 26: 325–329.

Werringloer, Anneliese. 1932. Die Sehorgane und Sehzentren der Dorylinen nebst Untersuchungen über die Facettenaugen der For-miciden. Zeitschr. wiss. Zool., 141: 432–524.

Wheeler, G. C. 1943. The larvæ of the army ants. Ann. Entom. Soc. Amer., 36: 319–332.

Wheeler, W. M. 1900. The female of *Eciton sumachrasti* Norton, with some notes on the habits of Texas Ecitons.[20] Amer. Nat., 34: 563–574.

[19] Redetermined as *E. burchelli*.

[20] Redetermined as *E. schmitti*.

————. 1910. Ants, their Structure, Development and Behavior. N. Y.:
          Columbia University Press. pp. 663.
————. 1921. Observations on army ants in British Guiana. Proc. Amer.
          Acad. Arts Sci., 56: 291–328.
————. 1925. The finding of the queen of the army ant *Eciton hamatum*
          Fabricius. Biol. Bull., 49: 139–149.
————. 1928. The social insects, their origin and evolution. N. Y.: Har-
          court, Brace.
———— AND I. W. BAILEY. 1920. The feeding habits of Pseudomyrminæ
          and other ants. Trans. Amer. Phil. Soc., 22, N.S., Art. 4: 235–279.
ZAHL, P. A. 1939. To the Lost World. N. Y.: Knopf.